A COMPARATIVE STUDY OF THE LARVAL MORPHOLOGY OF THE BRITISH PORTUNID CRABS *MACROPIPUS PUBER* (L.) AND *M. HOLSATUS* (FABRICIUS), WITH A DISCUSSION OF GENERIC AND SUB-FAMILIAL LARVAL CHARACTERS WITHIN THE PORTUNIDAE

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Pp. 121–151; 9 *Text-figures*; 9 *Tables*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 28 No. 4
LONDON: 1975

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 28, *No.* 4, *of the Zoological series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation :
Bull. Br. Mus. nat. Hist. (Zool.)

ISSN 0007–1498

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 29 *May,* 1975 *Price £1·90*

A COMPARATIVE STUDY OF THE LARVAL MORPHOLOGY OF THE BRITISH PORTUNID CRABS *MACROPIPUS PUBER* (L.) AND *M. HOLSATUS* (FABRICIUS), WITH A DISCUSSION OF GENERIC AND SUB-FAMILIAL LARVAL CHARACTERS WITHIN THE PORTUNIDAE

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SYNOPSIS

The zoeal and megalopa stages of two portunid crabs, *Macropipus puber* and *M. holsatus*, are described from material reared in the laboratory. Comparison of these larvae with one another and with those of *M. holsatus*, the only other species of the genus described in detail, indicates that while the larvae of the *Macropipus* species are all very similar there are clear distinctions between them.

The larval information available for the family as a whole generally supports the currently accepted sub-divisions within the Portunidae based on adult characters, but further detailed larval descriptions, particularly of those sub-families of which the larval stages are at present unknown, would probably help in the interpretation of phylogenetic relationships both within the family and between the portunids and the remainder of the Brachyura.

INTRODUCTION

THIS paper is the second in what is hoped will be a series describing the larval development of the British portunid crabs. The first paper (Rice and Ingle, 1975) described larvae reared from British specimens of the shore crab, *Carcinus maenas*, and compared them with those of the closely related Mediterranean form. This second paper deals with two of the eight species of the genus *Macropipus* which have been recorded from British waters.

Although Lebour's (1928, 1944) classic work on the Plymouth Brachyura established distinctions between the larvae of several genera and species of British crabs, she was not able to separate satisfactorily the larval and young stages of the *Macropipus* species with which she dealt (under the name *Portunus*) except on the basis of chromatophore pattern. Since that time the larvae of only one species of *Macropipus* have been reared and described in detail (Goldstein, 1971), but with a further two species described here it is now possible to discuss the nature of the specific larval characters within the genus.

MATERIALS AND METHODS

The ovigerous female *Macropipus puber* was obtained from Lulworth Cove, Dorset, in September 1972 and the *M. holsatus* from Port Erin, Isle of Man, in

February 1973. In both cases the crabs were maintained in sea-water at a temperature of 15 °C and all the larvae were reared at this temperature.

The eggs of *M. puber* hatched on 25 September 1972 and those of *M. holsatus* on 27 February 1973 and both broods were reared partly in mass culture and partly individually in compartmented plastic boxes (see Rice and Ingle, 1975). All of the larvae were fed on a mixture of *Prorocentrum* and freshly hatched *Artemia* nauplii.

The survival rate through the larval stage was quite good in both species, but was somewhat better in *holsatus* than in *puber* ; of 90 individually reared *M. holsatus* 25 (about 22 per cent) reached at least the first crab stage, whereas of 180 individually reared *M. puber* only 17 (about 9 per cent) reached this stage.

Although there was considerable individual variation in the number of days spent in each larval stage the total length of the larval life in both species was very similar, *M. holsatus* moulting into the first crab stage 43–53 (mean 48) days after hatching while *M. puber* reached this moult in 46–56 (mean 50) days.

The reared larvae and the females from which they were obtained are deposited in the British Museum (Natural History) under registration numbers 1974 : 333 (*M. holsatus*) and 1974 : 334 (*M. puber*).

MORPHOLOGY OF THE LARVAL STAGES AND SPECIFIC DISTINCTIONS WITHIN THE GENUS *MACROPIPUS*

The larvae of *Macropipus puber* and *M. holsatus* are illustrated in Figs. 2–9. The illustrations are supplemented in Tables 1–6 where these two species are compared with Goldstein's (1971) description of the larvae of *M. marmoreus*.

As was to be expected from previous work, the larvae of all three species are very similar, but although no single character separates them at all stages there are clear distinctions between them.

Thus the zoeae of *puber* differ from the other species at all stages in having straight rather than curved dorsal and rostral spines, and in the early stages by being considerably larger (Fig. 1*A–C*). This size difference becomes less marked in the later stages but at this time, that is in the fourth and fifth stages, an obvious distinction is the loss in *puber* of one of the spines on the telson forks. The larvae of *puber* are also consistently relatively narrower than those of *holsatus* and, at least in stage I, of *marmoreus* too (Fig. 1*D*). The absence of the relevant width data in Goldstein (1971) precludes the inclusion of *marmoreus* in this comparison beyond the first stage, specimens of which are deposited in the British Museum (Natural History).*

As in the adults (see Christiansen, 1969), the larvae of *holsatus* and *marmoreus* are more difficult to separate on morphological grounds, both of them having curved carapace spines and being similar in size. However, there are a number of fairly easily seen differences. First, the posterio-lateral processes on the abdominal somites are much better developed in *marmoreus* than in either *holsatus* or *puber*, particularly in the late zoeal stages. Secondly, with the possible exception of stage III, *marmoreus* resembles *puber* and differs from *holsatus* in having the spinous process

*Stage V larvae of *M. marmoreus* subsequently received from Dr Goldstein are intermediate between *puber* and *holsatus* in this respect.

of the antenna much shorter relative to the rostral spine. Finally, the lateral knobs on the third abdominal somite are lost in stage II in *marmoreus*, that is one stage earlier than in either *holsatus* or *puber*.

In addition to these characters there are less obvious differences, particularly between the zoeae of *marmoreus* on the one hand and *puber* and *holsatus* on the other, in the number of aesthetascs on the antennules and the setation of the antennae, maxillae and maxillipeds (see Tables 1–5).

The megalopae of the three species are also very similar. Although the comparative size situation is now the reverse of that in the early zoeal stages, the megalopae of *puber* tending to be smaller than those of either *holsatus* or *marmoreus*, the size ranges overlap a good deal. Similarly, while the megalopae of *holsatus* seem to have a rather lighter build than those of the other two species, this distinction is not very clear and in any case is obscured by the distortion resulting from preservation. There are, however, good distinctions between the species based on the antennae and telson. Thus, while *puber* has an antennal flagellum of seven segments and a telson with three pairs of dorsal setae, *holsatus* has eight segments in the flagellum and only two pairs of dorsal telson setae, and *marmoreus* has six segments in the antennal flagellum and four pairs of dorsal telson setae. Finally, the slender dactyl of the fifth pereiopod in *puber*, with its sub-terminal sensory setae, is clearly distinguishable from the broader dactyl and terminal setae of *holsatus* and *marmoreus*.

Although the features dealt with here clearly enable the larvae of *Macropipus puber*, *M. holsatus* and *M. marmoreus* to be differentiated, it is not possible to anticipate which of these characters, if any, will be of use in distinguishing between the other species of the genus. However, the fact that such consistent differences exist, particularly between the larval stages of *holsatus* and *marmoreus* which are so similar as adults, indicates that when the larvae of these other species are described in sufficient detail similarly clear distinctions will be found between them.

GENERIC AND SUB-FAMILIAL LARVAL DISTINCTIONS WITHIN THE FAMILY *PORTUNIDAE*

Previous attempts to define generic and sub-familial distinctions amongst portunid larvae have been clouded by the unfortunate nomenclatural confusion surrounding this family of crabs (see Opin. Decl. *Int. Commn zool. Nom.* 1956, vol. 12, Opinion 394, pp. 317–336). This confusion was primarily due to the use of the name *Portunus* for two distinct genera, one mainly confined to European waters, and the other widely distributed in the tropics and sub-tropics. The International Commission's decision was to retain the name *Portunus* Weber, 1795, for the widely distributed genus, which had also been called *Neptunus* in the Mediterranean and Indo-West-Pacific, and to adopt the name *Macropipus* Prestandrea, 1833, for the European genus. These changes have had repercussions in the nomenclature of the sub-familial divisions within the Portunidae, but the situation was clarified by Stephenson and Campbell (1960) whose interpretation and nomenclature, based on adult characters, are followed here except that the sub-family name Polybiinae Ortmann, 1893, is used in place of their Macropipinae.

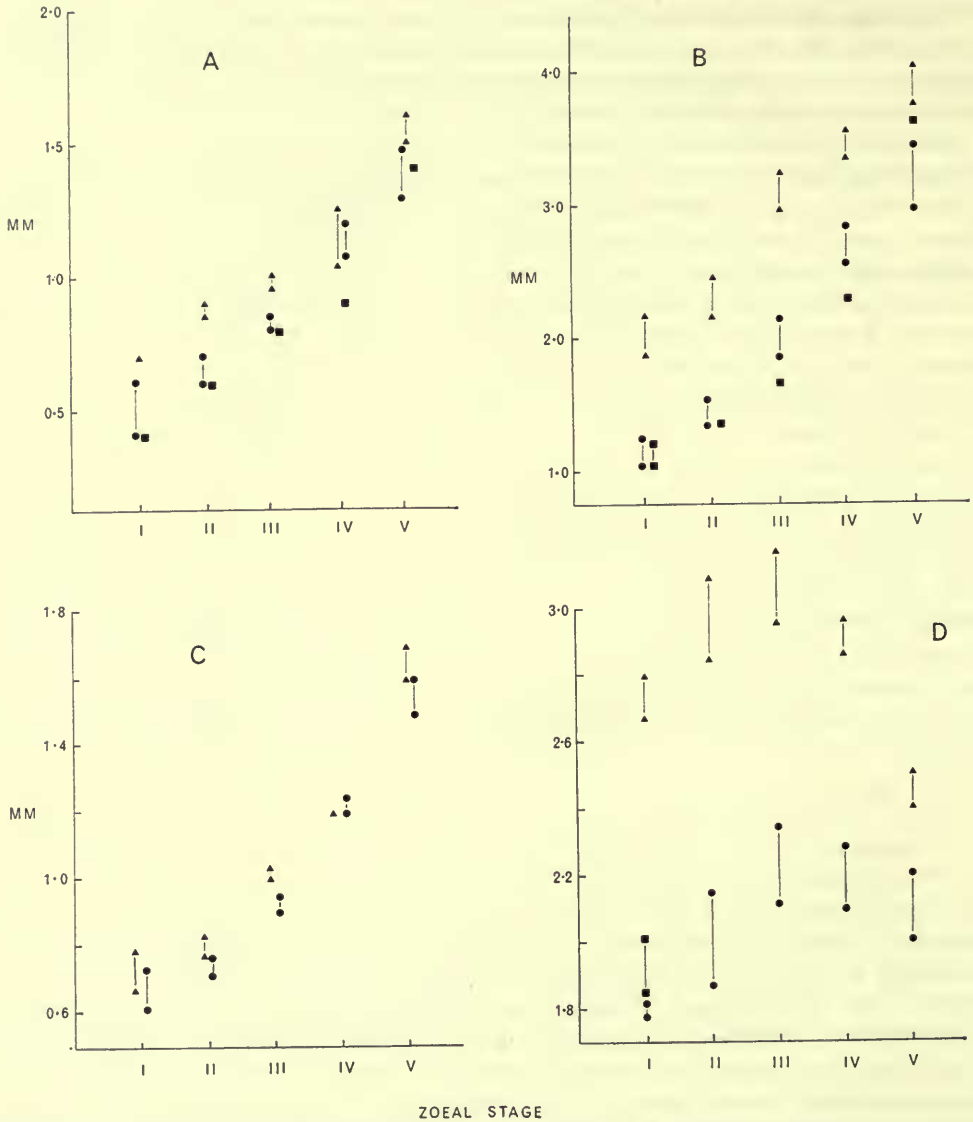

FIG. 1. A comparison of the dimensions of the zoeal stages of *Macropipus puber* (triangles), *M. holsatus* (circles) and *M. marmoreus* (squares). (*A*) Carapace length, (*B*) distance from the tip of the dorsal spine to the tip of the rostrum, (*C*) distance between the tips of the lateral carapace spines, and (*D*) ratio *B*/*C*.

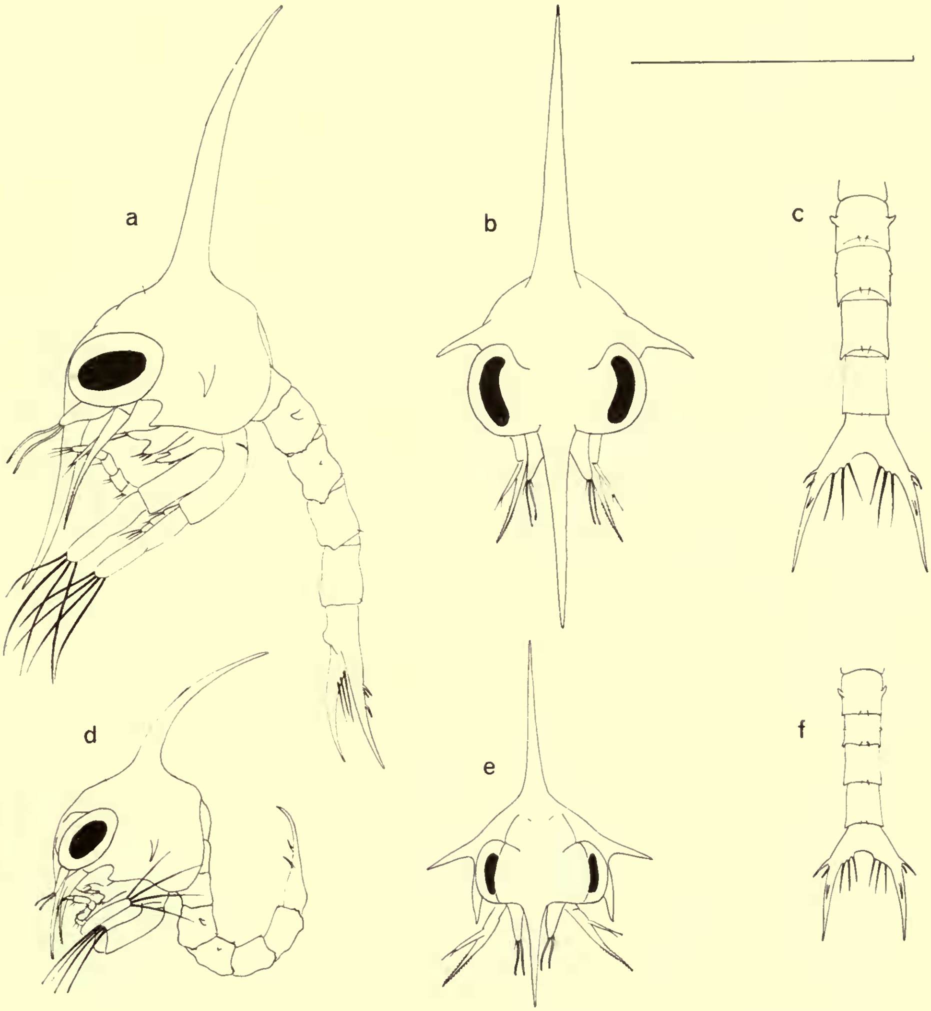

FIG. 2. First zoea of *M. puber* (*a*, *b* and *c*) and of *M. holsatus* (*d*, *e* and *f*). The bar scale represents 1·0 mm.

Stephenson and Campbell recognized six sub-families (Carcininae, Polybiinae (= Macropipinae), Portuninae, Catoptrinae, Caphyrinae and Podophthalminae), but larvae of only the first three of these are known. Apart from *Macropipus*, larvae of only two polybiinid genera have been described in detail ; *Ovalipes ocellatus* (Herbst) was reared through the zoeal stages and the megalopa by Costlow and Bookhout (1966), the megalopa of *O. punctatus* was described by Muraoka (1969), while Roberts (1969) reared *Bathynectes superba* (Costa) to the terminal zoea.

(*Continued on page 142*)

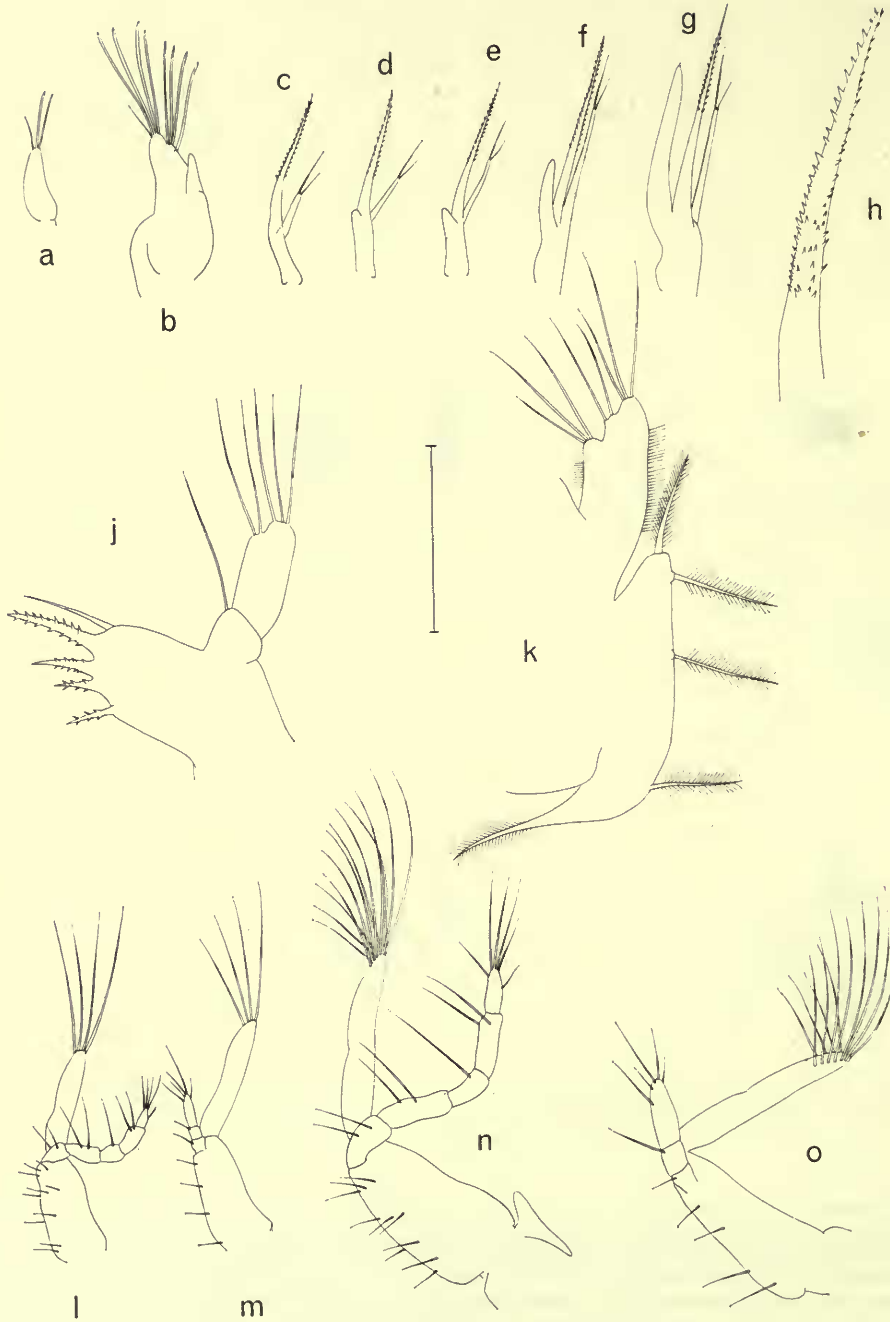

Fig. 3. Appendages of the zoeae of *M. puber*; (*a*) antennule, stage I, (*b*) antennule, stage II, (*c–g*) antenna, stages I–V, (*h*) detail of spinous process, stage I, (*j*) endopod and basal endite of maxillule, stage I, (*k*) endopod and scaphognathite of maxilla, stage II, (*l* and *m*) first and second maxillipeds, stage I, (*n* and *o*) first and second maxillipeds, stage V. The bar scale represents 0·1 mm for *h*, *j* and *k*, and 0·5 mm for the remainder.

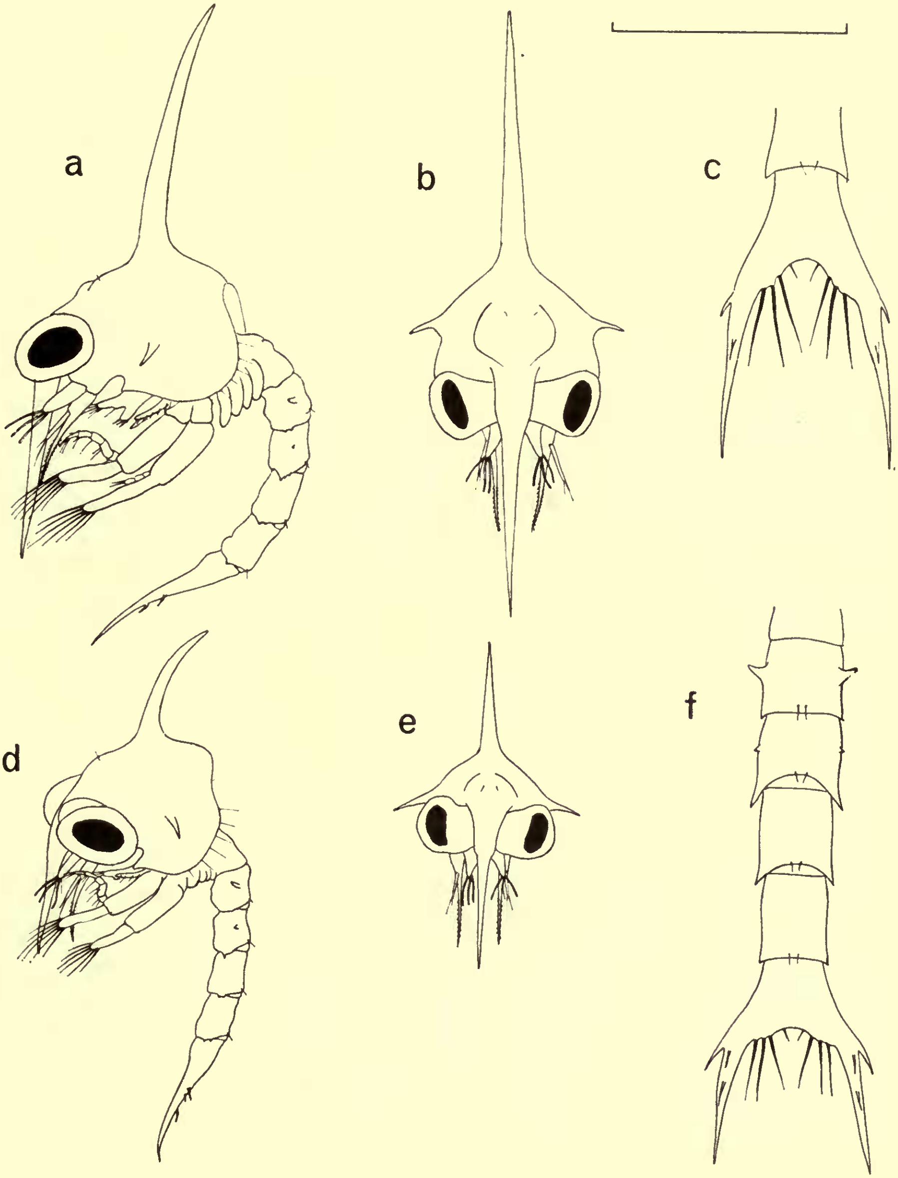

FIG. 4. Second zoea of *M. puber* (*a*, *b* and *c*) and of *M. holsatus* (*d*, *e* and *f*). The bar scale represents 1·0 mm.

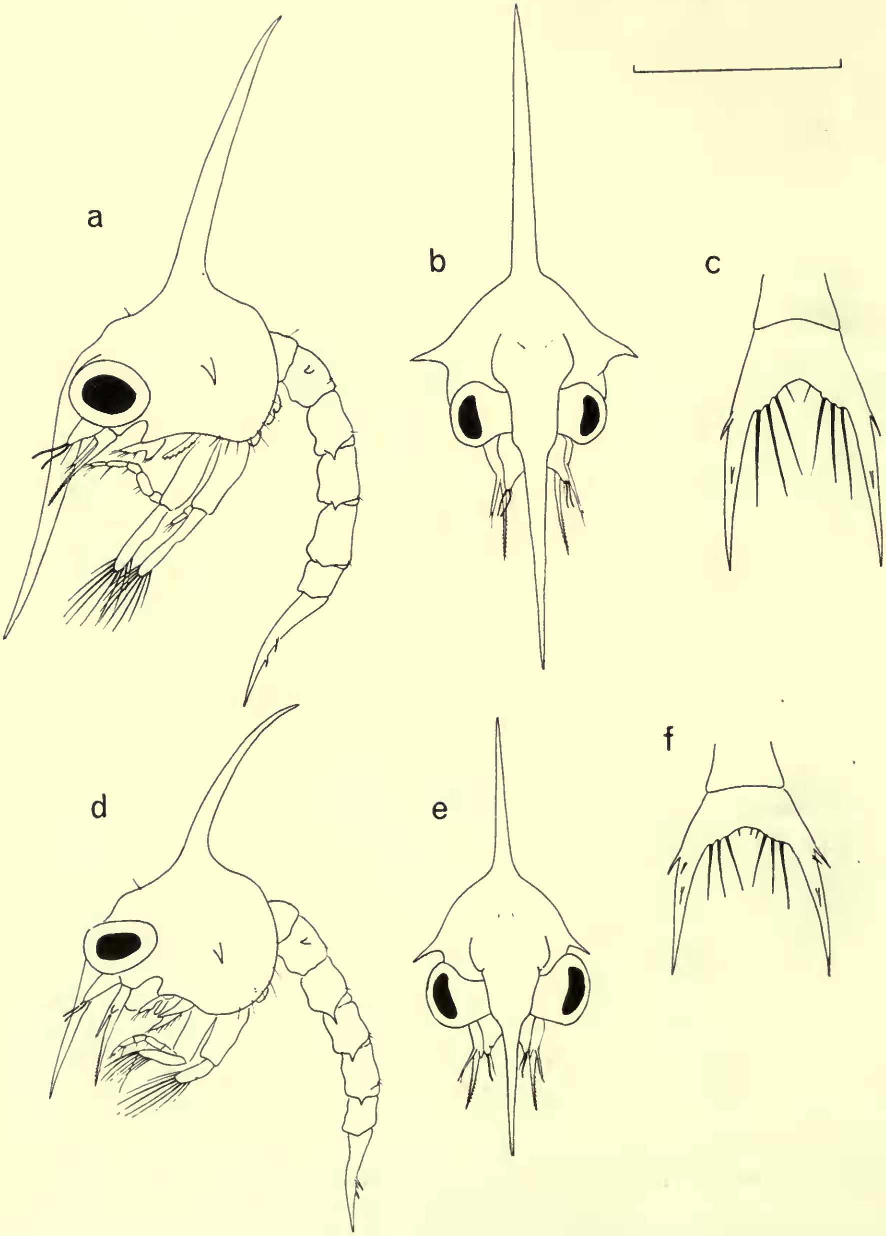

FIG. 5. Third zoea of *M. puber* (*a*, *b* and *c*) and of *M. holsatus* (*d*, *e* and *f*). The bar scale represents 1·0 mm.

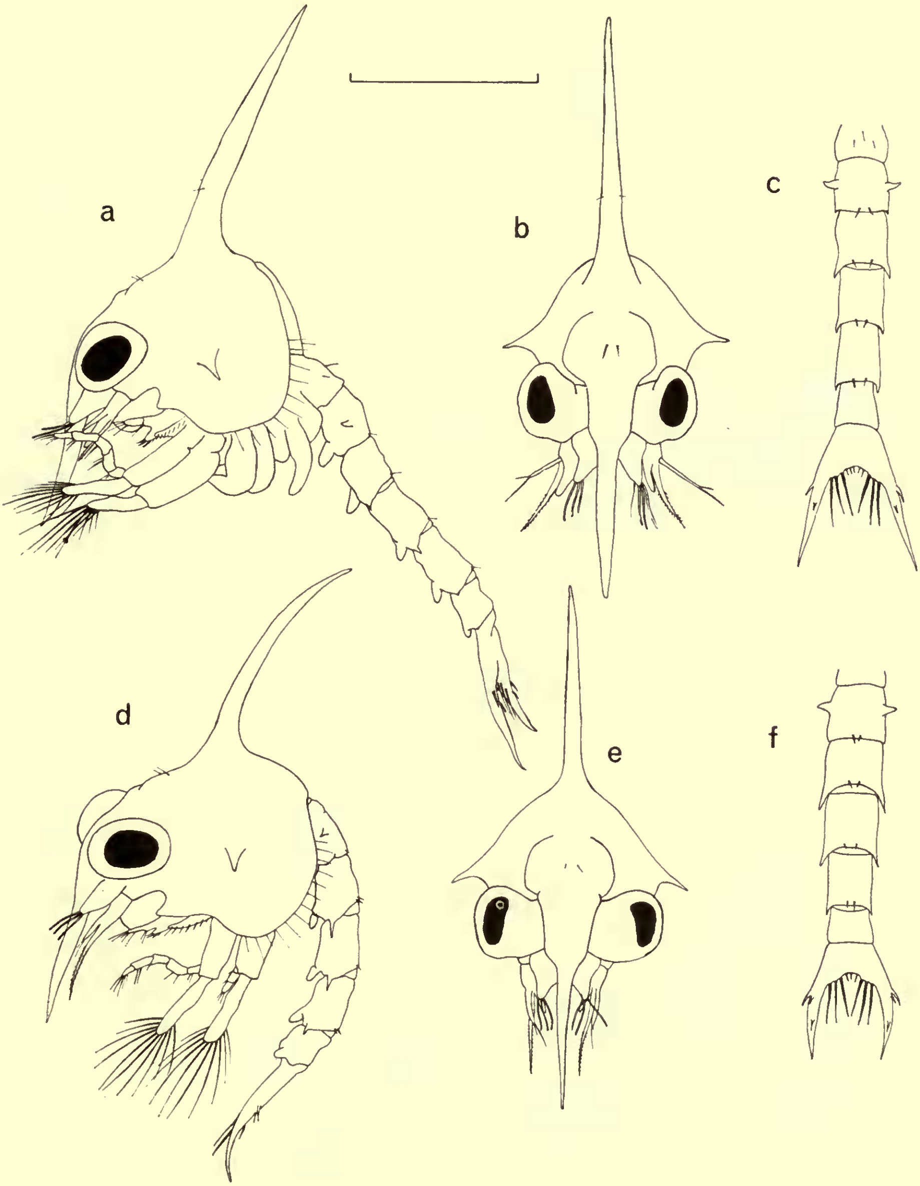

FIG. 6. Fourth zoea of *M. puber* (*a*, *b* and *c*) and of *M. holsatus* (*d*, *e* and *f*). The bar scale represents 1·0 mm.

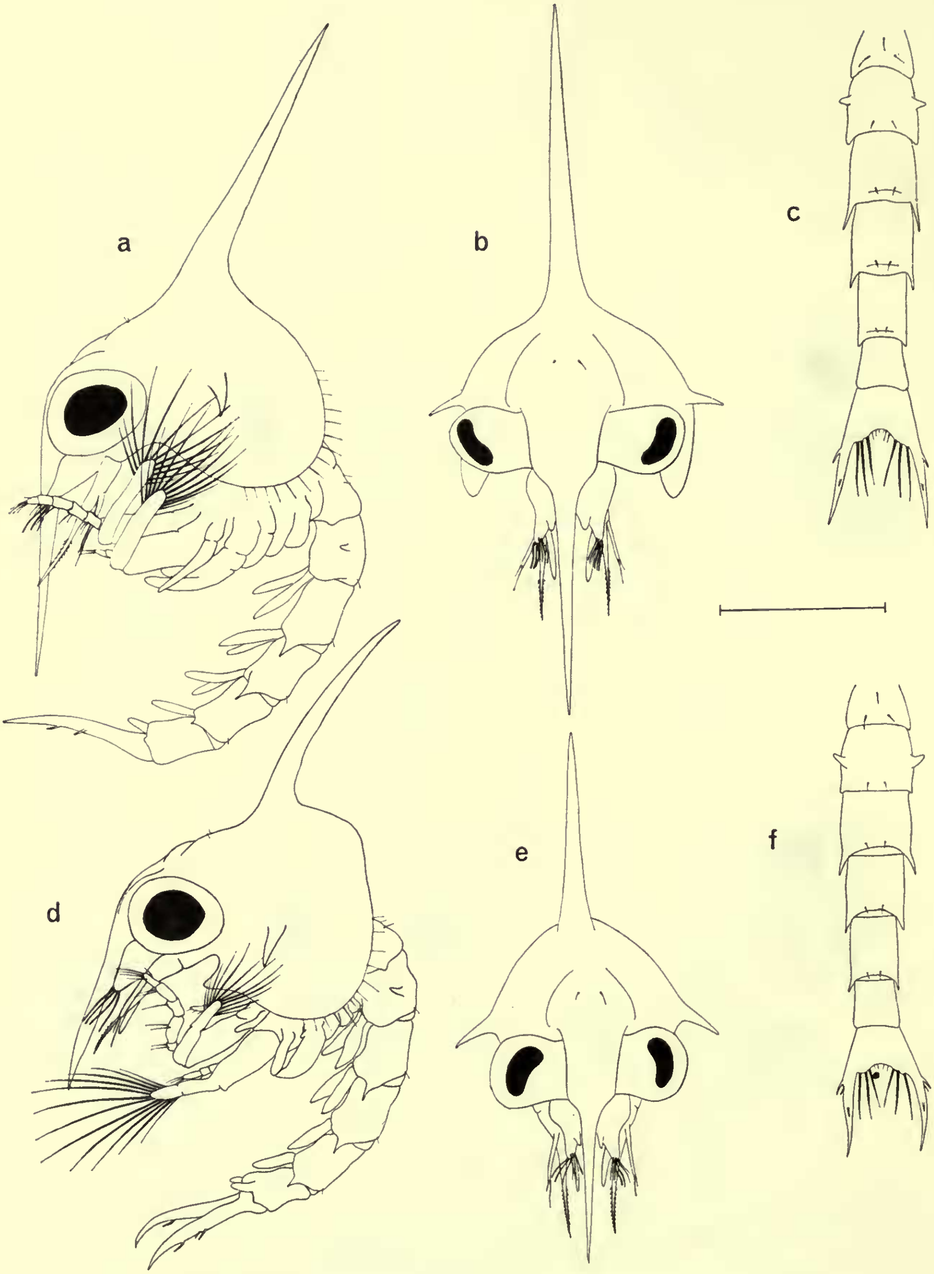

FIG. 7. Fifth zoea of *M. puber* (*a*, *b* and *c*) and of *M. holsatus* (*d*, *e* and *f*). The bar scale represents 1·0 mm

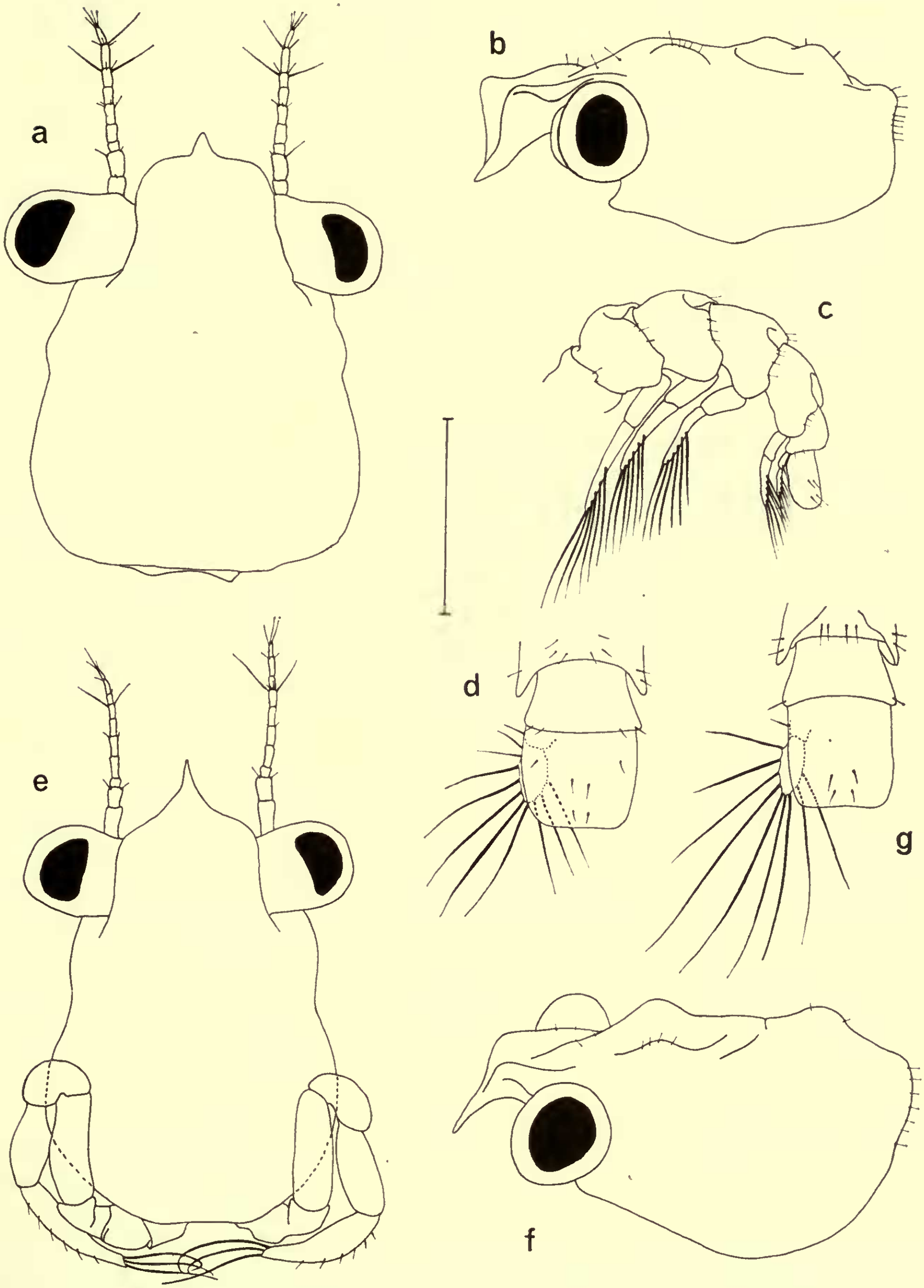

FIG. 8. Megalopa of *M. puber* (*a–d*) and of *M. holsatus* (*e–g*). The bar scales represent 0·5 mm for (*d*) and (*g*) and 1·0 mm for the remainder.

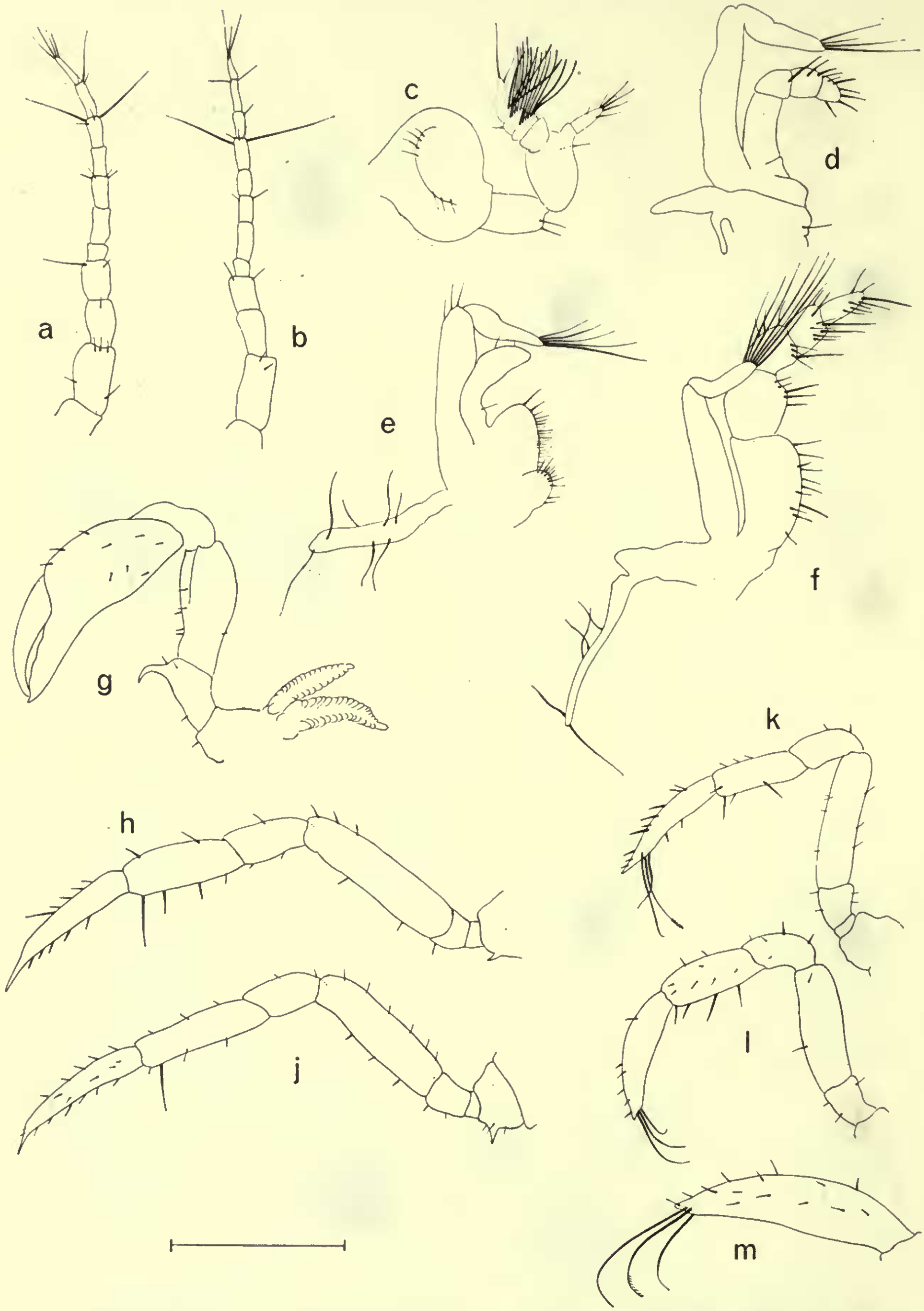

FIG. 9. Appendages of the megalopa stage in *M. puber* and *M. holsatus*: (*a*) antenna, *M. puber*; (*b*) antenna, *M. holsatus*; (*c*) antennule, *M. puber*; (*d, e* and *f*) first, second and third maxillipeds, *M. puber*; (*g*) cheliped, *M. holsatus*; (*h, j*) second and fourth pereiopods, *M. puber*; (*k*) fifth pereiopod, *M. puber*; (*l* and *m*) fifth pereiopod, *M. holsatus*. The bar scale represents 0·5 mm for *a–f* and *m*, and 1·0 mm for *g–l*.

TABLE 1

A comparison of the first zoeal stage in *Macropipus puber*, *M. holsatus* and *M. marmoreus**

M. puber	*M. holsatus*	*M. marmoreus**
	SIZE	
Carapace length : 0·7 mm	0·4–0·6 mm	0·4 mm
Tip of dorsal to tip of rostral spines (*a*) : 1·9–2·2 mm	1·1–1·3 mm	1·1 mm (1·18–1·24 mm†)
Width including lateral spines (*b*) : 0·67–0·78 mm	0·61–0·74 mm	– (0·58–0·67 mm†)
Ratio *a*/*b* : 2·68–2·80	1·80	– (1·84–2·0 mm†)
Length of dorsal spine : 0·9 mm	0·4–0·5 mm	0·5 mm
	CEPHALOTHORAX	
Carapace : Dorsal spine stout, straight or slightly curved at tip, much longer than carapace. Rostral spine straight or slightly curved anteriorly, longer than carapace. Lateral spines well developed. Carapace dorsal surface minutely rugose. Eyes sessile (Fig. 2*a*, *b*)	Dorsal spine slender, strongly curved posteriorly and equal to or only slightly longer than carapace. Rostral spine straight or curved backwards, equal to or shorter than carapace. Lateral spines well developed. Carapace smooth. Eyes sessile (Fig. 2*d*, *e*)	Similar to *holsatus*
Antennule : Unsegmented, with 2–3 terminal aesthetascs and 1–3 setae (Fig. 3*a*)	As *puber*	As *puber*
Antenna : Spinous process less than ¾ length of rostral spine. Exopod almost ½ length of spinous process, with 2 unequal terminal setae (Fig. 3*c*)	Spinous process about as long as rostral spine. Otherwise as *puber*	Exopod with 3 terminal setae. Otherwise as *puber*
Mandible : without palp	As *puber*	As *puber*
Maxillule : Endopod with 5 or 6 setae on distal segment and 1 on proximal segment. Basal endite with 5 setae, coxal endite with 6 setae (Fig. 3*j*)	As *puber*	As *puber*
Maxilla : Endopod bilobed with 6–8 setae, basal endite with 6–8 setae, coxal endite with 7 setae. Scaphognathite with 5 setae, posterior one largest (Fig. 3*k*)	As *puber*	Scaphognathite with 6 setae ; otherwise as *puber*
First maxilliped : Basipodite with 10 setae (2, 2, 3, 3), 5-segmented endopod with 2, 2, 1, 2 and 5 setae, exopod with 4 natatory setae (Fig. 3*l*)	As *puber*	Basipodite with only 6 setae ; otherwise as *puber*

M. puber	*M. holsatus*	*M. marmoreus**
Second maxilliped: Basipodite with 4 setae, 3-segmented endopod with 1, 1 and 4 or 5 setae, exopod with 4 natatory setae (Fig. 3*m*)	As *puber*	As *puber*
Pereiopods: Limb buds just visible beneath carapace	Not visible	Not visible
	ABDOMEN (Fig. 2*c*, *f*)	
Five somites plus telson. Somites 2 and 3 with lateral processes, those of somite 3 minute	As *puber*	As *puber*
Somites 2–5 each with pair of minute dorsal setae and with posterio-lateral margins with rounded expansions bearing small spinules	As *puber*	As *puber*, but posterio-lateral expansions on somite 3 more prominent and acute
Telson with 2 lateral and 1 dorsal spines on each fork; posterior margin with 3 pairs of setae	As *puber*	As *puber*

* The data on *Macropipus marmoreus* in Tables 1–6 are taken from Goldstein, 1971.
† Figures from material deposited in the British Museum (Natural History).

TABLE 2

A comparison of the second zoeal stages in *Macropipus puber*, *M. holsatus* and *M. marmoreus*

M. puber	*M. holsatus*	*M. marmoreus*
	SIZE	
Carapace length: 0·85–0·90 mm	0·60–0·70 mm	0·60 mm
Tip of dorsal to tip of rostral spines (*a*): 2·2–2·5 mm	1·40–1·60 mm	1·40 mm
Width including lateral spines (*b*): 0·77–0·84 mm	0·71–0·76	–
Ratio *a*/*b*: 2·85–3·01	1·87–2·15	–
Length of dorsal spine: c 1·0 mm	0·50–0·60 mm	0·50 mm
	CEPHALOTHORAX	
Carapace: As in stage I but eyes now stalked (Fig. 4*a*, *b*)	Similar to stage I but dorsal spine less than carapace length and eyes stalked (Fig. 4*d*, *e*)	As *holsatus*
Antennule: 4–6 aesthetascs and 1–3 setae	As *puber*	As *puber*
Antenna: Endopod present as a bud. Spinous process $< \frac{3}{4}$ length of rostral spine. Exopod with 2 terminal setae (Fig. 3*d*)	As *puber*, but spinous process almost as long as rostral spine	As *puber*, but exopod with 3 terminal setae

M. puber	*M. holsatus*	*M. marmoreus*
Mandible : As in stage I	As *puber*	As *puber*
Maxillule : Endopod as in stage I. Endites with additional setae. Exopod seta present	As *puber*	As *puber*
Maxilla : Endopod as in stage I. Endites with additional setae. Scaphognathite with 11 setae, posterior one no longer significantly different	As *puber*	As *puber*
First maxilliped : Exopod with 6 natatory setae ; otherwise as in stage I	As *puber*	Basipodite with 8 setae ; otherwise as *puber*
Second maxilliped : Endopod terminal segment with 4 setae. Exopod with 6 natatory setae	As *puber*	Endopod terminal segment with 5 setae. Otherwise as *puber*
Pereiopods : Limb buds prominent	Limb buds just visible	As *holsatus*
	ABDOMEN (Fig. 4*c, f*)	
Lateral processes on somite 3 present	As *puber*	Absent
Posterio-lateral processes of abdominal somites acute but not prominent	As *puber*	Posterio-lateral processes of somites 2–4 more prominent
One lateral spine on telson fork very small or absent	All 3 spines on telson forks well developed	As *holsatus*
Posterior telson margin with 4 pairs of setae	As *puber*	As *puber*

TABLE 3

A comparison of the third zoeal stages in *Macropipus puber*, *M. holsatus* and *M. marmoreus*

M. puber	*M. holsatus*	*M. marmoreus*
	SIZE	
Carapace length : 0·96–1·0 mm	0·80–0·85 mm	0·70 mm
Tip of dorsal to tip of rostral spine (*a*) : 3·0–3·3 mm	1·90–2·20 mm	1·70 mm
Width including lateral spines (*b*) : 1·00–1·04 mm	0·90–0·95 mm	–
Ratio *a*/*b* : 2·95–3·17	2·10–2·34	–
Length of dorsal spine : 1·40 mm	c 0·85 mm	0·70 mm
	CEPHALOTHORAX	
Carapace : As in stage II (Fig. 5*a, b*)	As in stage II but dorsal spine now equal to or slightly greater than carapace length (Fig. 5*d, e*)	As *holsatus*

M. puber	*M. holsatus*	*M. marmoreus*
	SIZE	
Antennule: As in stage II	As in stage II	As in stage II
Antenna: Endopod bud almost ⅓ length of exopod. Spinous process c ½ length of rostral spine. Exopod with 2 terminal aesthetascs (Fig. 3*e*)	As *puber* but spinous process > ¾ length of rostral spine	Endopod bud almost ⅓ length of exopod. Exopod with 4 terminal setae. Otherwise as *holsatus*
Maxillule: Additional setae on endites. Otherwise as in stage II	As *puber*	As *puber*
Maxilla: Scaphognathite with 13–14 setae	As *puber*	As *puber*
First maxilliped: Exopod with 8 natatory setae. Otherwise as in previous stages	As *puber*	As *puber*
Second maxilliped: Exopod with 8 natatory setae. Endopod terminal segment with 4 setae	Endopod with 3 terminal setae. Otherwise as *puber*	Endopod with 5 terminal setae. Otherwise as *puber*
	ABDOMEN (Fig. 5*c*, *f*)	
Sixth somite separated from telson	As *puber*	As *puber*
Lateral processes of somite 3 now absent	As *puber*	As *puber*
Posterio-lateral processes of somites 3–5 less than ¼ length of succeeding somites	More prominent, those on somite 3 about ⅓ length of somite 4	Similar to *holsatus*
Telson forks usually with only 2 spines; if third spine present it is minute	Telson forks each with 3 spines	As *holsatus*
Posterior telson margin with 4 pairs of setae	4 or 5 pairs of setae	5 pairs of setae

TABLE 4

A comparison of the fourth zoeal stages in *Macropipus puber*, *M. holsatus* and *M. marmoreus*

M. puber	*M. holsatus*	*M. marmoreus*
	SIZE	
Carapace length: 1·04–1·24 mm	1·10–1·20 mm	0·9 mm
Tip of dorsal to tip of rostral spine (*a*): 3·40–3·60 mm	2·60–2·90 mm	2·0 mm
Width including lateral spines (*b*): c 1·20 mm	1·20–1·25 mm	–
Ratio *a*/*b*: 2·86–2·96	2·10–2·29	–
Length of dorsal spine: 1·30–1·40 mm	1·10–1·20 mm	0·90 mm

M. puber	*M. holsatus*	*M. marmoreus*
	CEPHALOTHORAX	
Carapace: As in stage III (Fig. 6*a*, *b*)	As in stage III (Fig. 6*d*, *e*)	As in stage III
Antennule: 3 or 4 aesthetascs and 1 or 2 setae. Ventral flagellum may be present as small bud	As *puber* (Fig. 0)	6 aesthetascs in two groups, plus a terminal seta
Antenna: Spinous process about ½ length of rostral spine. Exopod ⅔ length of spinous process, with 2 terminal setae. Endopod ½ exopod (Fig. 3*f*)	Spinous process > ¾ length of rostral spine. Exopod < ½ spinous process, with 2 terminal setae. Endopod ⅔ exopod	Spinous process ½–⅔ rostral spine. Exopod < ½ spinous process, with 3 terminal setae. Endopod < ½ exopod
Maxillule: Additional setae on endites. Otherwise as in previous stage	As *puber*	As *puber*
Maxilla: Scaphognathite with about 25 marginal setae	As *puber*	As *puber*
First maxilliped: Endopod segments with 2, 2, 1, 2 and 6 setae. Exopod with 10 natatory seta	As *puber*	As *puber*
Second maxilliped: 10 natatory setae. Otherwise as in stage III	10 natatory setae. Endopod with 4 terminal setae, i.e. as in *puber*	10 natatory setae. Endopod with 5 terminal setae
Pereiopods: First leg now clearly chelate	As *puber*	As *puber*
	ABDOMEN (Fig. 6*c*, *f*)	
Posterio-lateral processes of somites 3–5 longer than in stage III, those of somite 3 about ¼ length of somite 4	More prominent than in *puber*, those of somite 3 about ⅓ somite 4	More prominent than in *holsatus*, those of somite 3 > ½ somite 4
Telson forks each with 2 spines	3 spines	3 spines
Posterior margin with 10 or 11 setae	Posterior margin with 9 or 10 setae	Posterior margin with 10 setae
Pleopods and uropods present as buds	As *puber*	As *puber*

TABLE 5

A comparison of the fifth zoeal stages in *Macropipus puber*, *M. holsatus* and *M. marmoreus*

M. puber	*M. holsatus*	*M. marmoreus*
	SIZE	
Carapace length: 1·50–1·60 mm	1·30–1·48 mm	1·50 mm
Tip of dorsal to tip of rostral spine (*a*): 3·8–4·1 mm	3·00–3·50 mm	3·70 mm
Width including lateral spines (*b*): 1·60–1·70 mm	1·50–1·60 mm	–
Ratio *a*/*b*: 2·4–2·5	2·0–2·2	–

M. puber	*M. holsatus*	*M. marmoreus*
	SIZE	
Length of dorsal spine : 1·60–1·70 mm	1·3 mm	1·40 mm
	CEPHALOTHORAX	
Carapace : As in previous stages (Fig. 7*a, b*)	As in previous stages (Fig. 7*d, e*)	As in previous stages
Antennule : 8–10 aesthetascs in 2 or 3 groups, plus a terminal seta. Ventral flagellum well developed (Fig. 3*b*)	As *puber*	13 aesthetascs plus terminal seta. Ventral flagellum well developed
Antenna : Spinous process about ½ length of rostral spine. Exopod about ½ length of spinous process ; 2 terminal setae. Endopod > exopod (Fig. 3*g*)	Spinous process > ¾ length of rostral spine. Otherwise as *puber*	Spinous process < ¾ rostral spine. Exopod < ½ spinous process ; 4 terminal setae. Endopod > exopod
Mandible : Palp now present	As *puber*	As *puber*
Maxillule : Similar to stage IV	As *puber*	As *puber*
Maxilla : Schaphognathite with 30–36 marginal setae	As *puber*	Scaphognathite with about 40 setae
First maxilliped : As in stage IV but with 12 natatory setae (Fig. 3*n*)	As *puber*	As *puber*
Second maxilliped : Endopod terminal segment with 5 setae. Exopod with 12 natatory setae (Fig. 3*o*)	Endopod terminal segment with 4 or 5 setae. Exopod with 12 natatory setae	As *puber*
Third maxilliped : Well developed, biramous but unarmed	As *puber*	As *puber*
Pereiopods : Limbs clearly segmented	As *puber*	As *puber* ?
	ABDOMEN (Fig. 7*c, f*)	
Posterio-lateral processes of somites 3 and 4 about ⅓ length of succeeding somites	As *puber*	Posterio-lateral process of somite 3 > ½ length of somite 4
Telson forks with 2 spines	3 spines	3 spines
Posterior margin with 10 or, more usually, 12 setae	10 setae	10 setae
Pleopods as long as succeeding somites	As *puber*	As *puber*

TABLE 6

A comparison of the megalopa stage in *Macropipus puber, M. holsatus* and *M. marmoreus*

M. puber	*M. holsatus*	*M. marmoreus*
	SIZE	
Carapace lenght (*a*) : 1·66–2·09 mm	1·86–2·16 mm	c 2·0 mm
Carapace width (*b*) : 1·57–1·76 mm	–	1·65 mm
Ratio *a*/*b* : 1·12–1·26	c 1·40	c1·22

M. puber	*M. holsatus*	*M. marmoreus*
	CEPHALOTHORAX	
Carapace: Relatively broad (see length/width ratio above). Rostrum directed ventrally and not prominent in dorsal view. Dorsal surface with two medial tubercles and two pairs of lateral ones. These tubercles, and particularly the posterior medial one, vary considerably in prominence. Front about ½ maximum carapace width. Posterior margin almost straight and meeting lateral margins in abrupt angles (Fig. 8*a*, *b*)	Relatively narrow. Rostrum generally directed more anteriorly than in *puber* and therefore more prominent in dorsal view. Posterior margin arched and not meeting the lateral margins in abrupt angles. Otherwise as *puber* (Fig. 8*e*, *f*)	Relatively broad. Rostrum prominent in dorsal view. Posterio-lateral tubercles absent. Front about ⅓ maximum carapace width
Antennule: Three-segmented peduncle. Dorsal flagellum of 4 segments with 2 terminal setae and 3 groups of aesthetascs (Fig. 9*c*)	As *puber*	As *puber*
Antenna: Peduncle of 3 segments and flagellum of 7 segments, the fifth bearing 2 long setae (Fig. 9*a*)	Flagellum of 8 segments (Fig. 9*b*)	Flagellum of 6 segments, the long setae being on the third
Mandible: Well-developed 2-segmented palp with 8–10 setae	As *puber*	As *puber*
Maxillule: Endopod of 2 segments carrying 2 and 4 setae respectively. Endites with many marginal spines and setae	As *puber*	As *puber*
Maxilla: Endopod unarmed or with a single seta. Schaphognathite with about 50 marginal setae	As *puber*	As *puber*
First maxilliped: Exopod with 3–5 setae on the proximal segment and 4 or 5 on the distal one. Endopod unsegmented and reduced. Well-developed epipod of fairly constant width throughout its length (Fig. 9*d*)	As *puber*	Epipod expanded basally. Otherwise as *puber*
Second maxilliped: Exopod 2-segmented, proximal with 1 small seta, distal with 4 or 5 terminal setae. Endopod 4-segmented, proximal naked. Epipod small (Fig. 9*e*)	As *puber*	As *puber*
Third maxilliped. Exopod with 6 terminal setae. Endopod of 5 segments, all armed. Epipod long (Fig. 9*f*)	As *puber*	As *puber*
Pereiopods. Cheliped with prominent curved spine on ischio-basis. Pereiopods 2–4 with straight spines on coxae (Fig. 9*g*, *h*, *j*)	Pereiopods 1–4 as in *puber*	Pereiopods 1–4 as in *puber*

M. puber	*M. holsatus*	*M. marmoreus*
	Cephalothorax	
Dactyl of pereiopod 5 slender, length more than 5 times maximum width. Sensory setae clearly sub-terminal. Coxal spine minute or absent (Fig. 9*k*)	Dactyl of pereiopod 5 broad, length about 4 times maximum width. Sensory setae virtually terminal (Fig. 9*l*, *m*)	As *holsatus*
	Abdomen (Fig. 8*c*)	
Somites 2–5 with posterio-lateral expansions rounded	As *puber*	As *holsatus*
Exopods of pleopods on somites 2–5 with 17–19, 16–19, 17–18 and 13–15 setae respectively	Exopods of pleopods with 17–20, 19–20, 18–19 and 14–16 setae respectively	?
Endopods of pleopods with 3, or rarely 4, coupling hooks	As *puber*	As *puber*
Exopods of uropods with 8–10 setae	9 or 10 setae	8 setae
Telson usually narrows posteriorly, but may be almost square. Posterior margin usually straight or slightly concave, but may be markedly so	Telson normally square, but may narrow posteriorly. Shape therefore not consistently distinguishable from *puber*	?
Telson dorsal surface with 2 pairs of posterio-medial setae arranged in a rectangle elongated longitudinally. Additional pair of anterio-lateral setae (Fig. 8*d*)	Telson dorsal surface with 2 pairs of posterio-medial setae arranged in a rectangle elongated transversely. No anterio-lateral setae (Fig. 8*g*)	Telson dorsal surface with 4 pairs of setae

Costlow and Bookhout mistakenly considered the species dealt with by Lebour (1928) under the name *Portunus* to belong to the sub-family Portuninae, so that with the exception of an inadequate account of the first zoeal stage of *Bathynectes longipes* Risso (Lebour, 1931) their description of the development of *Ovalipes ocellatus* seemed to be the first of a true polybiinid. Their discussion of possible sub-familial larval characters within the Portunidae was therefore largely invalid, but they nevertheless recognized the possession of sternal cornua in the megalopa stage as a portuninid character (see below). Roberts was similarly confused by the generic nomenclature when he compared his reared *Bathynectes* larvae with those of other species in the family and consequently did not recognize some larval differences which seem to be generic or even sub-familial.

On the other hand, Goldstein (1971) did not mix polybiinid and non-polybiinid species in her comparison with the larvae of *Macropipus marmoreus*, and was able to point out several differences between *M. marmoreus*, *Ovalipes ocellatus* and *Bathynectes superba*. The additional information presented here on the larvae of *M. puber* and *M. holsatus* now warrants a more detailed comparison in order to establish the sort of generic distinctions which are likely to obtain between larval Polybiinae. The three genera *Macropipus*, *Ovalipes* and *Bathynectes* are therefore compared in Tables 7 and 8, revealing differences which at the moment appear to be generic.

TABLE 7

A comparison of the zoeal stages in *Macropipus*, *Bathynectes* and *Ovalipes*

	*Macropipus**	*Bathynectes†*	*Ovalipes‡*
ABDOMEN			
Dorso-lateral processes, somite 3	Stages I and II only	All stages	All stages
Dorso-lateral processes, somite 4	Absent	Absent	Present stages I–III
Dorso-lateral processes, somite 5	Absent	Absent	Present all stages
Posterio-lateral processes, somite 4	$<\frac{1}{2}$ somite 5	$>\frac{1}{2}$ somite 5 from stage II	$<\frac{1}{2}$ somite 5
TELSON			
Telson fork armature, stage I	3 spines (1 dorsal)	3 spines (1 dorsal)	2 (both lateral)
Telson fork armature, stages II–V	2–3 (1 dorsal)	3 (1 dorsal)	2 (both lateral)
Anterior lateral telson spine	$<\frac{1}{4}$ fork length	$>\frac{1}{4}$ fork length	$<\frac{1}{4}$ fork length
Posterior margin, stage II	4+4 setae	3+3	3+3
Posterior margin, stage III	5+5 setae	4+4	4+4
FIRST MAXILLIPED			
Basipodite medial setae	6–10	10	4–?
Endopod terminal setae, stage III	5	6	6
Natatory setae, stages II–V	6, 8, 10, 12	6, 8, 10, 12	7, 8, 10, 14
SECOND MAXILLIPED			
Natatory setae, stages II–V	6, 8, 10, 12	6, 8, 10, 12	7, 10, 12, 15

* Based on *Macropipus puber* and *M. holsatus* described in this paper, and on *M. marmoreus* described by Goldstein, 1971.
† Based on *Bathynectes superba* described by Roberts, 1969.
‡ Based on *Ovalipes ocellatus* described by Costlow and Bookhout, 1966.

TABLE 8

A comparison of the megalopa stage in *Macropipus* and *Ovalipes*

	Macropipus spp.	*Ovalipes ocellatus**	*Ovalipes punctatus*†
Lateral knobs on carapace	Absent	Present	Absent
Rostral spine	Directed downwards‡	Directed forwards	Directed forwards
Coxal spines on legs 2–4	Present	Absent	Absent
Maxillule endopod, basal segment	2 setae	3 setae	2 setae
Maxilla endopod	Unarmed or with a single seta	7 setae	6 setae
Maxilliped 1, endopod	Unsegmented, expanded at tip with 3–6 setae	Segmented, not expanded, about 17 setae	Unsegmented, with about 17 setae
Dactyl, pereiopod 5	Not markedly flattened ; L : W>4 : 1	Markedly flattened ; L : W<3·5 : 1	As *O. ocellatus*
Abdominal somite 5, posterio-lateral margins	Rounded	?	Acute
Pleopods, endopods	3–4 hooks	?	7 hooks
Pleopods, exopods	13–20 marginal setae	?	31–40 marginal setae
Uropods, proximal segment	0–1 seta	?	3 setae
Uropods, distal segment	8–10 marginal setae	?	About 22 marginal setae

* Data from Costlow and Bookhout, 1966.
† Data from Muraoka, 1969.
‡ Except *depurator* according to Lebour (1928).

In the zoeal phase *Ovalipes* can be distinguished from the other two genera by the possession of dorso-lateral processes on the fifth abdominal somite in all stages and on the fourth somite up to stage III, and in lacking a dorsal spine on the telson forks. *Macropipus* differs from both *Ovalipes* and *Bathynectes* in losing the dorso-lateral process on the third abdominal somite after the second stage, while in all the zoeal stages *Bathynectes* has much longer posterio-lateral processes on the fourth somite and also a much more prominent anterior spine on the telson fork than either *Macropipus* or *Ovalipes*.

Unfortunately Roberts was unable to obtain the megalopa of *Bathynectes* so that in this stage *Macropipus* can be compared only with *Ovalipes*, and even here much of the information which would be useful in such a comparison is not available (see Table 8). Nevertheless, the megalopae of *Ovalipes* seem to differ from all described *Macropipus* megalopae in having more setose appendages, particularly the abdominal ones, and in lacking the prominent spines on the coxal segments of legs 2, 3 and 4.

Possible sub-familial characters of the Polybiinae can be discussed only in relation to the Carcininae and the Portuninae, for which at least some larval information has been obtained. Within the Carcininae, although Couch hatched and described the first zoea of the common and widely distributed shore crab, *Carcinus maenas* (L.), as early as 1844 and there were many subsequent accounts of some or all of the larval stages of this species, they have only recently been described in detail from reared material and compared with the closely related *C. mediterraneus* Czerniavsky (see Rice and Ingle, 1975). The only other carcininid genus of which larvae are known is *Portumnus*, Lebour (1944a) having hatched and reared the first two stages of *P. latipes* and attributed to the same species a plankton-caught terminal zoea which moulted to the megalopa and then to the first crab stage in the laboratory. Another plankton-caught megalopa which moulted to a first crab had been ascribed to *Xavia biguttata* (Risso) (as *Portumnus biguttatus*) in an earlier paper (Lebour, 1928) ; these two megalopae were very distinct.

There are many morphological details, particularly in the setation of the appendages, in which the larvae of *Carcinus* and *Portumnus* differ from those of the polybiinid species discussed above. Some of these features may be good sub-familial characters, but in addition there are a number of much more obvious differences which appear to enable larval carcininids to be distinguished readily from polybiinids. Firstly, the two *Carcinus* species, and probably also *Portumnus*, pass through only four zoeal stages, whereas all the known polybiinids have five zoeae. The consequent differences in developmental rates result in distinct combinations of characters in the two sub-families ; pleopod buds, for instance, occur on zoeae with 8 natatory setae on the exopods of the maxillipeds in the Carcininae, that is in the third stage, whereas the pleopods do not appear in the Polybiinae until the fourth zoeae in which the maxillipeds carry 10 setae. This character would not, of course, enable stage I and II carcininid and polybiinid larvae to be separated, but the zoeae of *Carcinus* and *Portumnus* differ from those of *Macropipus* in these early stages, and from those of *Bathynectes* and *Ovalipes* at all stages, in having no dorso-lateral processes on the third abdominal somite. Carcininid zoeae also differ from the polybiinids, certainly from the third stage, in having only three pairs of setae on the posterior margin of the telson, whereas all the known larval *Macropipus*, *Bathynectes* and *Ovalipes* add at least one extra pair of setae and often more. But the most obvious carcininid zoeal character, which distinguishes them from all other known portunids, both polybiinids and portuninids (see below), is the total absence of lateral carapace spines.

In the megalopa stage *Carcinus* and *Portumnus* differ from *Macropipus* in having no coxal spines on pereiopods 2–4, and from *Ovalipes* in having rounded posterio-lateral margins to the fifth abdominal somite. Both polybiinid genera differ from *Carcinus* in having more setae on the pleopods and uropods, the difference being more marked in *Ovalipes* than in *Macropipus*.

In terms of the number of species of which larvae have been described, the Portuninae is the best known sub-family of swimming crabs. However, although there are published accounts of one or more stages of five portuninid genera, many of these accounts are inadequate, several are based on material collected from the plankton and therefore of doubtful identity and, of the reared species, the complete development is known for only four (see Table 9). Nevertheless, the available data do allow some general comments about portuninid larvae to be made.

TABLE 9

Descriptions of larval Portuninae referred to in the accompanying discussion*

SPECIES	STAGE(S)	SOURCE OF MATERIAL	AUTHOR
Callinectes sapidus	Zoeae I–VII, megalopa	Hatched and reared	Costlow and Bookhout, 1959
Scylla serrata	Zoeae I–V, megalopa	Hatched and reared	Ong, Kah Sin, 1964
Scylla serrata	Zoea I	Hatched	Naidu, 1955
Charybdis acuta	Zoeae I–VI, megalopa	Hatched and reared	Kurata and Omi, 1969
Charybdis japonica	Zoeae I–VI, megalopa	Hatched and reared	Yatsuzuka, 1952
Charybdis lucifera	Zoea I	Hatched	Hashmi, 1970
Charybdis annulata	Zoea I	Hatched	Hashmi, 1970
Charybdis callianassa	Zoea I	Hatched	Hashmi, 1970
Charybdis orientalis	Zoea I	Hatched	Hashmi, 1970
Charybdis 6-dentata	Zoea I	Plankton	Aikawa, 1937
Charybdis bimaculata	Zoea IV, megalopa	Plankton	Aikawa, 1937
Portunus trituberculatus	Zoea I	Hatched	Aikawa, 1937
Portunus pelagicus	Zoea I, megalopa	Plankton	Aikawa, 1937
Portunus pelagicus	Zoea I	Hatched	Delsman and De Man, 1925
Portunus pelagicus	Zoeae I–IV, megalopa	Hatched and reared	Yatsuzuka, 1962
Portunus pelagicus	Zoeae I, II and III ?	Hatched and plankton	Prasad and Tampi, 1953
Portunus sayi	Zoea I ?	Plankton	Lebour, 1944b
Portunus depressifrons	Zoea I ?	Plankton	Lebour, 1944b
Thalamita crenata	Zoea I	Hatched	Prasad and Tampi, 1953
Thalamita sima	Megalopa	Plankton	Muraoka, 1969
Portunus sanguinoleutus	Zoea I	Plankton	Chhapgar, 1956
Portunus pelagicus	Zoea I	Plankton	Chhapgar, 1956
Charybdis orientalis	Zoea I	Plankton	Chhapgar, 1956
Thalamita crenata	Zoea I	Plankton	Chhapgar, 1956

* The list is by no means complete, a number of publications having been omitted because the identifications are particularly unreliable, the descriptions are inadequate or they have been superseded by subsequent work. A more serious omission, however, is the excellent account of the larval development of *Portunus spinicarpus* by Bookhout & Costlow (1974), which was not seen until after this manuscript had been submitted. Fortunately, *P. spinicarpus* is a typical portuninid and its omission does not affect the discussion of sub-familial larval characters in this paper.

Firstly, there is considerably more variation in the rate of development in the portuninids than in either the polybiinids or carcininids, the number of zoeal stages ranging from seven in *Callinectes sapidus* through six in *Charybdis acuta* and *C. japonicus*, five in *Scylla serrata*, to four in *Portunus pelagicus* (or even three, according to Prasad and Tampi, 1953, although the sizes given for their zoeae indicate that they may have missed at least one stage). This heterogeneity extends also to some morphological features, such as the telson fork armature, for while there is a tendency to a reduction of the number of spines on the telson forks in the later stages of portuninids, just as in the other two sub-families, there is considerable variation even in the first zoeal stage. Thus while some species (e.g. *Scylla serrata*, *Portunus depressifrons* and *P. sayi*) retain all three spines on each fork, one of the lateral spines is reduced to a fine hair in *Charybdis callianassa*, *C. lucifer* and *C. annulata*, and totally disappears in *Portunus trituberculatus*, *P. pelagicus*, *P. sanguinolentus*, *Callinectes sapidus*, *Charybdis japonicus*, *C. 6-dentata*, *C. orientalis* and *Thalamita crenata*. Finally, Chhapgar (1956) illustrates only a single spine on the telson forks of his larvae of *Charybdis orientalis*, *Thalamita crenata*, *Portunus sanguinolentus* and *P. pelagicus*.

This variability allows the zoeae of individual portuninid species to be distinguished fairly easily from all known polybiinids, but there does not seem to be a single feature which will separate the two sub-families at all zoeal stages. For those characters which are common to all portuninid zoeae, such as the possession of well-developed dorsal, rostral and lateral carapace spines, dorso-lateral processes on abdominal somites 2 and 3, posterio-lateral processes on somites 3–5 in the later stages, telson forks usually with at least two spines of which one is dorsal, and the addition of at least one extra pair of setae on the posterior margin of the telson from stage II, are almost without exception shared also with some or all of the polybiinids. In fact, the only feature we have noticed which seems to be unique to portuninid zoeae is the absence of any setae on the middle segment of the endopod of the first maxilliped in the first zoeal stage.* [Hashmi (1970) figures a seta in this position in the first zoea of *Charybdis callianassa*, but we have been unable to confirm its existence in material deposited by him in the collections of the British Museum (Natural History).] Even this fine distinction disappears in the later stages of *Scylla serrata* and *Charybdis acuta*, and as early as the second zoea in *Callinectes sapidus*, and would hardly seem sufficient to support the sub-familial separation of the Portuninae and Polybiinae based on adult characters. But in the megalopa stage there are much clearer distinctions between the Portuninae, on the one hand, and all other described swimming crabs, on the other. All portuninid megalopae, for instance, have prominent posterio-lateral spines on the fifth abdominal somite which are found only in *Ovalipes punctatus* amongst the Carcininae and Polybiinae. Similarly, there is a tendency in the Portuninae to increase the number of setae on the uropods beyond that found in the other two families, again with the exception of *Ovalipes*, but since this armature ranges in *Portunus pelagicus* from 10 or 11 (according to Aikawa, 1937, and Yatsuzuka, 1962) to 20 (according to Prasad and Tampi, 1953) the reliability of this character is very doubtful. By far the most striking portuninid megalopal character, however, is the possession of a pair of prominent posterio-ventrally directed spines, the so-called sternal cornua, arising from the sternum between the last pair of legs. This feature at once distinguishes the portuninids, not only from the carcininids and polybiinids, including *Ovalipes*, but also from all other brachyuran megalopae so far described.

These differences between the larvae of the Carcininae, the Polybiinae and the Portuninae are summarized in the following diagnoses.

* One other possibly unique portuninid zoeal character is the position of the pair of fine setae on the dorsal surface of the carapace. In the Carcininae and Polybiinae these setae are anterior to the dorsal spine and close together, whereas in the Portuninae they are between the dorsal and lateral carapace spines. However, they may not always be present, for Costlow and Bookhout, 1959, specifically looked for them in *Callinectes* and failed to detect them.

Carcininae
ZOEAE

Four zoeal stages ; carapace without lateral spines ; dorso-lateral projections on abdominal somite 2 only ; posterio-lateral processes of abdominal somites 3 and 4 less than half length of succeeding somites in all stages ; telson fork armature reduced to a single spine in late stages ; telson posterior margin with 3+3 setae in all stages ; middle segment of endopod of first maxilliped armed with a single seta in stage I.

MEGALOPA

Rostrum directed forwards or downwards ; no coxal spines on pereiopods ; no sternal cornua ; pleopods with 9–12 (rarely 13) marginal setae ; uropods with 4–10 marginal setae ; posterio-lateral spines on abdominal somite 5 absent.

Polybiinae
ZOEAE

Five zoeal stages ; well-developed lateral carapace spines ; dorso-lateral projections on abdominal somites 2 and 3, at least in the early stages ; posterio-lateral processes of abdominal somites 3 and 4 usually less than half length of succeeding somites in later stages ; telson forks with at least 2 spines in all stages ; telson posterior margin with at least 4+4 setae in late stages ; middle segment of endopod of first maxilliped armed in stage I.

MEGALOPA

Rostrum directed forwards or downwards ; coxal spines on pereiopods 2–4 present (*Macropipus*) or absent (*Ovalipes*) ; no sternal cornua ; pleopods with 14–20 (rarely 13) marginal setae (*Macropipus*) or 31–40 (*Ovalipes*) ; uropods with 8–10 marginal setae (*Macropipus*) or c 22 (*Ovalipes*) ; posterio-lateral spines on abdominal somite 5 absent (*Macropipus*) or present (*Ovalipes*).

Portuninae
ZOEAE

Four to seven zoeal stages ; well-developed lateral carapace spines ; dorso-lateral projections on abdominal somites 2 and 3 in all stages ; posterio-lateral processes of abdominal somites 3 and 4 more than half length of succeeding segments in late stages ; telson forks with at least 2 spines in all stages (except according to Chhapgar) ; telson posterior margin with at least 5+5 setae in late stages ; middle segment of endopod of first maxilliped unarmed in stage I.

MEGALOPA

Rostrum directed forwards ; coxal spines absent from pereiopods 3 and 4 but may be present on pereiopod 2 (*Charybdis* and *Scylla*) ; sternal cornua always present ;

pleopods with 17–26 marginal setae ; uropods with 11–14 marginal setae ; posterio-lateral spines of abdominal somite 5 always prominent and usually over-reaching somite 6.

THE BEARING OF LARVAL CHARACTERS ON PORTUNID CLASSIFICATION

The above distinctions between the larval stages of the Carcininae, Polybiinae and Portuninae generally support the current divisions within the family which are based largely on the degree to which the adults show adaptations to the swimming habit. These adaptations include a tendency to lighten the integument, to flatten the carapace and extend it laterally to improve the dynamics of sideways swimming, to change the orientation of the leg articulations and to flatten the limbs and fringe them with setae to produce effective paddles (Hartnoll, 1971). There is a good deal of variation in the extent of these adaptations within the sub-families, but in general the Carcininae and Portuninae represent the extreme conditions, the Carcininae showing the least and the Portuninae the most modification from the unspecialized brachyuran form. The Polybiinae are somewhat intermediate between the other two sub-families and even within the genus *Macropipus* there is a considerable range in swimming adaptations, and particularly in the degree of flattening of the legs (see Palmer, 1927).

This situation is reflected in the larvae, for while the Carcininae and Portuninae exhibit major differences in both the zoea and megalopa stages, the Polybiinae have zoeae which resemble the Portuninae while the megalopae are more similar to those of the Carcininae. This does not, of course, necessarily mean that the Polybiinae stand phylogenetically between the Carcininae and the Portuninae, and the presence in the zoeae of *Ovalipes* of characters such as the dorso-lateral processes on abdominal somites 4 and 5, which are apparently unique amongst the portunids, indicates that this genus, at least, is well away from any such route.

It has been generally accepted that the swimming adaptations of adult portunids are secondary acquisitions and that the relative absence of such adaptations in the Carcininae is therefore a primitive condition. There have, however, been suggestions that the morphological series into which extant swimming crabs can be arranged might be read in the opposite direction, so that the loss of swimming adaptations becomes an advanced feature (Palmer, 1927; Lebour, 1928). The information available from the larval stages does not provide any clear evidence for one or other of these views. For the main character distinguishing carcininid larvae from all other portunids, that is the absence of lateral carapace spines in the zoeal stages, occurs sporadically in a number of other brachyuran families and does not seem to be of any particular phylogenetic importance. On the other hand, the presence of sternal horns on all portuninid megalopae, a feature which is unique not only amongst the Portunidae but also amongst the Brachyura generally, indicates that this sub-family probably represents the end of a portunid evolutionary line rather than an intermediate stage.

It is possible, of course, that the Polybiinae are phylogenetically more 'primitive' than either the Carcininae or the Portuninae, in the sense that they are closer to the ancestral stock or stocks of both sub-families. This would require two parallel evolutionary tendencies within the Portunidae, one involving a loss of swimming adaptations and a return to the relatively unspecialized brachyuran condition of the Carcininae, and the other leading to the increased specialization of the Portuninae.

Morphological details of the larvae of more swimming crab species, and particularly those of the sub-families of which the larval stages are totally unknown at present, might help to clarify these relationships within the Portunidae and between the swimming crabs and other brachyuran families. But the pelagic larvae are generally much more similar than the adults since they show none of the specializations for such habits as swimming, burrowing or commensalism which characterize the benthic adult phase. A study of larval systematics will therefore probably require a numerical approach, making use of a much greater variety of features than has usually been used in the past. Such an investigation is underway at the moment using the available published information for all brachyuran larvae, and it is hoped that this will not only supplement the systematics based on adult characters but will also help in the identification of unknown plankton-caught larvae.

ACKNOWLEDGEMENTS

We wish to thank Trevor Davies and members of the Guildford Branch of the British Subaqua Club for collecting the female *M. puber* and Dr D. I. Williamson, Port Erin Marine Biological Station, for obtaining for us the material of *M. holsatus*.

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